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## Vulnerability of melanic *Daphnia* to brown trout predation

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**Abstract.** The co-existence of melanic *Daphnia cf. longispina* and facultatively planktivorous brown trout is reported from a clear-water, alpine lake. This co-occurrence is uncommon, presumably due to the vulnerability of pigmented *Daphnia* to fish predation. Lake Bjornesfjorden (Norway) provided an opportunity to test this assumption. About 20% of the fish caught in gill nets had fed on *Daphnia*. The trout exerted a marked selection for large-sized *Daphnia* prey, and a very strong selection for pigmented individuals relative to transparent ones. The persistence of a pigmented *Daphnia* population probably relies on limited recruitment and a low stock of the predator, and the availability of more favourable benthic prey organisms.

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### Introduction

Cuticular pigments in *Daphnia* are known to provide protection from harmful UV radiation (Hebert and Emery, 1990; Hessen and Sørensen, 1990; Hobæk and Wolf, 1991; Hessen, 1993, 1994). These melanin pigments are deposited in the dorsally directed parts of the exoskeleton. In contrast to internal pigments like carotenoids, cuticular pigments are lost with every moult and have to be replenished in the newly formed carapace tissue. Melanic *Daphnia* are well known within the *D.pulex* group, primarily from arctic habitats (e.g. Brooks, 1957; Hebert and McWalter, 1983; Weider *et al.*, 1987; Hobæk *et al.*, 1993), and within the *D.longispina* group, which is known from both alpine and arctic habitats (Hobæk and Wolf, 1991; Taylor and Hebert, 1994).

The geographical distribution and local occurrence of melanic species and clones indicate that pigmented lineages are highly vulnerable to predation by fish, due to their visual conspicuousness relative to unpigmented variants. This assumption is well founded in theory and empirical observations on visual selection in fish (Zaret, 1980). Apart from body size alone, any colour that increases visibility is generally expected to increase the selectivity of a visually feeding fish for a particular food item. Examples include pigmented eggs, eyes (Zaret, 1972) and ehippia (Mellors, 1975) in cladocerans, and carotenoid pigments in copepods (Hairston, 1979; Luecke and O'Brien, 1981). Nonetheless, the assumption of increased vulnerability of melanic *Daphnia* to fish predation remains untested in a field situation. This is probably due to the fact that co-occurrence of melanic *Daphnia* with fish is uncommon.

Here we present the results of a field study that provided the opportunity to

document clear selectivity for the pigmented individuals of a *Daphnia* cf. *longispina* population, superimposed on normal size selectivity. The study was conducted in a shallow, clear-water alpine lake with virtually no littoral vegetation. No temperature stratification occurred and Secchi transparency exceeded lake depth. Hence, the abiotic conditions of the lake provided no refuge from fish predation for the zooplankton population.

## Method

Lake Bjornesfjorden (17 km<sup>2</sup> surface area) is situated at 1223 m a.s.l., on the Hardangervidda mountain plateau (60°10'N, 7°41'E) in Norway. Most of this clear-water lake is shallower than 6 m and a Secchi disk was easily visible at this depth during the study period in August. Water temperature was 8.2°C throughout the water column. The lake hosts a relatively low-numbered population of large-sized brown trout (*Salmo trutta* L.), which has been harvested for centuries. The yield from commercial net catches was estimated at 1.53 kg ha<sup>-1</sup> in 1989 (Tysse and Garnås, 1990), and the average length of commercially netted fish was 34 and 38 cm for stocked and wild trout, respectively (L'Abée-Lund and Sægrov, 1991).

The data were collected during test fishing in August 1989, ~40 days after ice-break. Fishing methods and results on fish stock composition were presented in L'Abée-Lund and Sægrov (1991). Zooplankton were sampled by vertical and horizontal net hauls (diameter of net 30 cm, mesh size 90 µm). Plankton samples were preserved in ethanol, as were samples of fish food contents. In addition to *Daphnia* cf. *longispina*, the crustacean zooplankton community included the cladocerans *Bosmina longispina* and *Sida crystallina*, the copepods *Cyclops scutifer*, *Mixodiaptomus laciniatus*, and *Heterocope saliens*.

From the net hauls, we measured total length (TL; from base of shell spine to top of head shield) and carapace length (CL; from base of shell spine to base of antennal insertion) in 200 *Daphnia* individuals by means of a dissecting microscope fitted with an ocular micrometer. The linear least-squares regression of TL on CL

$$TL = 1.216CL + 0.097 \quad (N = 198, R^2 = 0.98, P < 0.001)$$

was then used to estimate TL in damaged *Daphnia* individuals in the stomach contents. A total of 101 fish stomachs were examined. Up to 20 *Daphnia* individuals per stomach were measured. Stomach contents were subsampled as necessary. Each *Daphnia* in the plankton and stomach samples was scored as transparent, intermediate or melanistic, based on its appearance under the microscope.

## Results

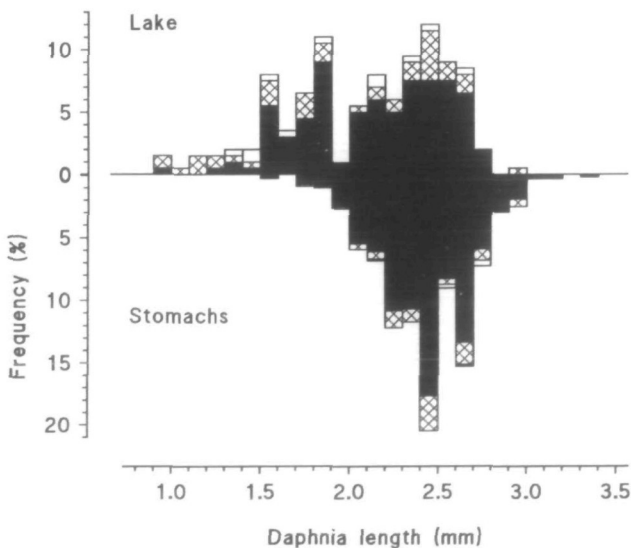
Melanistic *Daphnia* constituted 73% of total *Daphnia* numbers in net hauls, while transparents made up a minor part (6%; Table I). The difference between these

**Table I.** Number, frequency (%) and lengths (arithmetic means, mm ± 95% confidence limits and ranges) of three pigment categories of *D. cf. longispina* in net hauls and brown trout stomachs from the alpine Lake Bjornesfjorden

Pigment category	Net hauls				Fish stomachs			
	<i>n</i>	Frequency	Mean	Range	<i>n</i>	Frequency	Mean	Range
Transparent	11	5.5	1.82 ± 0.31	1.27–2.55	7	1.0	2.49 ± 0.21	2.02–2.70
Intermediate	44	22.0	1.87 ± 0.17	0.90–2.85	73	10.9	2.39 ± 0.07	1.61–3.30
Melanic	145	72.5	2.05 ± 0.06	0.86–2.66	593	88.1	2.32 ± 0.02	1.50–3.07
Total	200	100.0	2.00 ± 0.04	0.86–2.85	673	100.0	2.33 ± 0.01	1.50–3.30

two categories was even more distinct in the brown trout stomachs with 88 and 1%, respectively. Thus, brown trout exerted a highly significant selection on fully melanic individuals (*G*-test, *P* < 0.001).

Within each pigmentation category, *Daphnia* from the net hauls demonstrated a larger range in size than in the fish stomachs. In the lake sample, there was a bimodality in the length distribution, indicating that at least two cohorts or age groups were present (Figure 1). Analysis of variance (ANOVA) of *Daphnia* length from the net hauls showed that a significant degree of heterogeneity existed among the three groups of pigmentation ( $F_{2,197} = 3.76, P < 0.05$ ). This was due to a larger body size in melanic individuals (Table I). The length of *Daphnia* from the fish stomachs also showed a significant degree of heterogeneity among the three categories of pigmentation ( $F_{2,670} = 3.63, P < 0.05$ ). However, in this case,



**Fig. 1.** Length distribution (%) of transparent (open bars), intermediate (cross-hatched) and melanic (dark) *D. cf. longispina* in net hauls (upper, *n* = 200) and brown trout stomachs (lower, *n* = 673), Lake Bjornesfjorden, 1989. The number of individuals within each category is given in Table I.

the transparent individuals were larger than the other groups. Irrespective of pigmentation, brown trout selected the larger individuals (ANOVA,  $P < 0.01$  for all groups; Table I, Figure 1).

## Discussion

Previous studies on population genetics in alpine populations of the *D. longispina* complex have revealed that melanic populations constitute a separate genetic entity, which probably is a distinct species (Hobæk and Wolf, 1991). Moreover, melanic and transparent lineages were never found to co-exist, probably because of competitive exclusion and differences in UV tolerance. However, melanic populations may contain a number of apparently transparent animals, which have recently moulted. Since cuticular pigments are lost with each exuvium, they have to be replenished in the newly formed exoskeleton. This process takes some time (at least 1 day at these temperatures; A.Hobæk, unpublished observation). Genetic analyses and direct observations confirm that such animals are in fact melanic (Hobæk and Wolf, 1991; Hobæk, unpublished observation). The proportion of apparently transparent individuals depends directly on moulting frequency, and ultimately on food availability and temperature. Hence, the occurrence of variability in pigmentation level in this *Daphnia* population is readily explained by a time lag in the deposition of melanin. In the absence of genetic analyses, however, we cannot rule out the co-existence of clones varying in pigmentation level in Lake Bjornesfjorden. Morphologically, the population appears homogenous. Although the population undoubtedly belongs within the *D. longispina* complex, its relation to established taxa within this group remains uncertain.

Brown trout in Lake Bjornesfjorden fed chiefly on *Gammarus lacustris* and *Lepidurus arcticus*, which together made up 96% in dry weight of the stomach contents (L'Abée-Lund and Sægrov, 1991). These prey were 50–100 times larger (milligrams dry weight) than *D. cf. longispina*, which made up 1.5% of total stomach contents. However, *Daphnia* were found in 20% of the brown trout stomachs with a mean number of 325 in each, demonstrating that it is an attractive prey. The presence of melanic *D. cf. longispina*, despite predation from planktivorous brown trout, in Lake Bjornesfjorden is most likely due to an overall low predation pressure from fish. Recruitment limitations, as well as regular harvesting, contribute to maintain a low fish stock in this lake (L'Abée-Lund and Sægrov, 1991).

A preference for larger prey is expected for brown trout (Langeland, 1978). In a recent study, Langeland and Nøst (1995) found this species capable of catching *Daphnia galeata* as small as 1.1 mm, and *B. longispina* down to 0.4 mm. Thus, almost the entire *Daphnia* population in Lake Bjornesfjorden is vulnerable to predation (Figure 1). The smallest individual eaten was 1.5 mm long. The size component of selectivity was most pronounced for transparent, and less so for pigmented, *Daphnia* prey (Table I). Melanic individuals were caught at smaller sizes than transparent ones. Hence, brown trout seem to select pelagic prey mainly by its visibility (or apparent size; O'Brien *et al.*, 1976).

Planktonic *Daphnia* populations often undertake diurnal vertical migrations to avoid visual predation (Lampert, 1989). Vertical migrations have also been observed in alpine populations (Hessen, 1993), and provide protection from UV radiation as well as fish predation. In shallow Lake Bjornesfjorden, there is no dark refuge in the depths, suggesting that diurnal migration is unimportant. In fact, numerous darkly pigmented animals could be observed by the naked eye at the surface even around noon. This is probably an important prerequisite for the persistence of a pigmented population, since if a depth refuge was available, unpigmented *Daphnia* clones might well outcompete the melanic lineage(s).

The adaptive value of melanin pigments in *Daphnia* is fairly well documented (Hebert and Emery, 1990; Hobæk and Wolf, 1991; Hessen, 1994). As previously assumed, this adaptation does indeed render the animals highly vulnerable to fish predation. The co-occurrence of fish and a pigmented *Daphnia* population in Lake Bjornesfjorden apparently depends on a balance between selection for pigment protection from UV irradiation and the intensity of fish predation. In this shallow lake, there is no spatial escape from either of these strong selective forces. If this is correct, we would expect to see a negative relationship between the densities of brown trout and melanic *Daphnia* in otherwise comparable lakes, and changes in the fish stock should be followed by changes in melanic *Daphnia* density.

### Acknowledgements

We are indebted to Gudrun Bakkerud and the late Metter Matre for sorting and measuring zooplankton. Thanks are also due to Harald Lura for help during the field work and for suggesting improvements to the manuscript. This study was supported by the Norwegian Research Council via the research program 'Dynamics and enhancement of freshwater fish populations'.

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Received on April 16, 1996; accepted on July 5, 1996